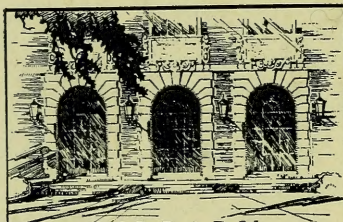


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COMPARATIVE STUDIES ON CERTAIN
FEATURES OF NEMATODES AND
THEIR SIGNIFICANCE

WITH FOUR PLATES AND SIX TEXT FIGURES

BY
DUNCAN CHARTERIS HETHERINGTON

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward
No. 223

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE
GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1922

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INTRODUCTION

The members of the phylum Nematoda both the parasitic and free living forms are exceptionally interesting in view of the varieties of structure existing in the cephalic region and also in view of the changes in structural symmetry from the fundamental bilaterality to pseudo-radial symmetry, true radial symmetry, and asymmetry.

In the following pages the author has directed his attention to a comparative study of the symmetry and structural variety of the cephalic regions existing among the nematodes, parasitic and free living, endeavoring throughout to determine the most primitive cephalic plan from which the most complicated forms were derived and the order of this derivation. Furthermore, some new and valuable methods of nematode technique have been devised to lessen the tedium and numerous difficulties involved in preparing this material for microscopical examination either as sections or toto-mounts and in addition, the question of ciliation among nematodes is discussed and evidence presented for the undoubted existence of such structures.

This comparative study was undertaken at the suggestion of Dr. Henry B. Ward, to whom the author at this time wishes to express his sincere thanks, not only for his interest in this study, but also for permission to use his private literature files and material from his collection of unnamed parasites. Further thanks are due to the other members of the department also for their kindly help and criticism.

SOME NEW METHODS OF NEMATODE TECHNIQUE

The difficulties involved in the preparation of nematodes for microscopical examination either as totes or sections can be appreciated fully only by those who have made any attempts whatsoever in that direction. Perhaps this fact has been one contributing in no small degree to the scarcity of workers in the field as compared with other fields of zoology and has at the same time been responsible in a measure for the confusion of nematode literature on systematic relations through the piling up of countless, meager, stereotyped descriptions, many of them based only on external appearances, gross anatomical features, and measurements. Few comprehensive studies exist on the gross and histological anatomy or upon physiological systems of the legion of nematodes known, comparable to the works of Looss on the life history and anatomy of the hookworm or of Martini on *Oxyuris curvula*.

The main points of a simplified and rapid technique suitable for the microscopical preparation of the larger free living and parasitic nematodes may be found in an article by the author (Hetherington 1922), the essentials of which will be repeated here for convenience, with the addition of a few suggestions and comments.

The greatest obstacle to successful nematode preparation is the almost impenetrable cuticula in which the animal is encased, as it were, offering a splendid barrier to the entrance of the ordinary fixatives and clearing media, particularly the resinous ones in which one often desires to mount specimens.

During a series of experiments with various killing and dehydrating fluids it was noticed that little collapse and crumpling took place in fluids containing acids as lactic and acetic. The liquids seemed to diffuse with greater ease through the cuticula if some agent were present which kept it soft and pliable during the stages of dehydration, especially between 85 per cent alcohol and the clearing agent where the greatest difficulty was always encountered. In every case of shrinkage and collapse the indications were that diffusion pressures caused the damage and that, were a series of dehydrating and clearing fluids possible which had very similar diffusibilities or penetrabilities, the greatly unbalanced diffusion pressures arising during the passage of the material from one liquid to the next would be eliminated and with them the distortion of the specimens.

By the use of Carnoy-phenol, itself water free, the killing and dehydration processes can be accomplished at once in the following way: The material freshly collected and freed from adhering dirt and slime is placed in

CARNOY-PHENOL

Absolute alcohol.....	20 cc
Chloroform.....	15 cc
Glacial acetic acid.....	5 cc
Phenol crystals to raise the volume by.....	10 cc
Total.....	50 cc

If the fluid is too strong for very delicate worms, it may be weakened by the addition of a very small quantity of water. After killing the worms should be placed in the fluid of full strength before further operations are undertaken. With material so killed only two operations are required to bring the objects into paraffin or balsam, and one to clear them in glycerine; if killed in other media and stored in alcohol, three operations attain the same end. Nematodes may be taken from 70 to 80 per cent alcohol, glycerine, lacto-phenol, or formol in which they have been stored and placed directly in the fluid. Smaller worms are cleared almost instantly so that a rapid survey if desired may be made of their internal

organization after which they may be removed to 95 or 80 per cent alcohol for storage. If the larger specimens do not clear sufficiently at first, almost any degree of clearing may subsequently be obtained by allowing the fluid in which the worms are placed to evaporate, the degree of clearing being proportional to the amount of evaporation. Still greater transparency is obtained by adding glacial acetic acid and phenol to the worms.

With specimens now in the fluid they may be prepared either for sectioning or for mounting in balsam with equal ease. Oils of synthetic wintergreen and oleum cidri ligni (Merk) or chloroform may be dropped *slowly* into the dish with the specimens and mixed thoroughly by agitation. The progress of this clearing should be watched carefully under a binocular or compound microscope and if the slightest shrinkage is observed it indicates that the clearing is being rushed. The change of liquids must be very gradual especially at first when the tissues are hardening but as soon as the mixture is three quarters clearing fluid, the greater part may be drawn off and the pure liquid added more rapidly and allowed to remain for 10 to 15 minutes or longer. If now infiltration by paraffin is desired, the wax is shaved into the dish with the specimens in clearing fluid and the whole set aside in a slightly warm place for 2 hours when the worms may be placed in pure paraffin, melting at 58 C. and after proper infiltration imbedded and sectioned.

Following Carnoy-phenol fixation numerous stains work nicely on sections, preferably those stains which do not require taking the sections to water because in such cases the cuticula is likely to swell and tear loose the sections or parts of them. Delafield's or Ehrlich's hematoxylin in 50 or 70 per cent alcohol stain well followed by Orange G or some other counterstain. Among the iron-hematoxylin's Dobell's works splendidly and is, for the reason mentioned previously, preferable to Heidenhain's, it is also more selective and does not require a watery mordant. Staining is accomplished in the following manner:

Sections are freed of paraffin and run down to 70 per cent alcohol in the usual way. At this point they are mordanted in 1 or 2 per cent solution of iron alum (ammonium ferric sulphate) in 70 per cent alcohol for one-half to one hour (or longer), rinsed in 70 per cent alcohol and placed in a 1 per cent solution of hematein in 70 per cent alcohol for a period as long as that of mordanting or longer. The sections after this treatment and rinsing in 70 per cent alcohol are ready for destaining which may be done rapidly in 0.5 per cent acid (HCl) in 70 per cent alcohol, but preferably, for more even results, in the mordant itself until satisfactory differentiation has taken place. The sections may be counterstained or not as one desires, cleared, and mounted in damar or in what is an excellent medium—cedar immersion oil.

Safranin O counterstained with lichtgrün produces a pleasing stain in which, however, the lichtgrün is dominant because of the few nuclei appearing in any one section of material. But the most pleasing stain of all for presenting differentiated pictures is obtained with Mallory's triple stain (Guyer 1917). By this combination of dyes all cuticular parts are colored in shades of blue to purple blue—with an occasional exception where it is orange red. Muscle tissue such as the contractile portions of the muscle cells of the body wall are brilliant red as also are the muscle fibres and bundles of the esophagus and other portions. Protoplasm is pink with a suggestion of a bluish tint; nuclei are darker red with brilliant orange nucleoli. Material fixed in Flemming's reagent and stained with Mallory shows less red with more yellow and purple shades; differentiation being even greater.

To mount whole preparations in balsam the procedure is the same as for sectioning, including the bringing of the worms into clearing fluid; wintergreen is here to be preferred to the other clearing fluids in general laboratory use because of its rapid penetrating power; xylol shrinks tissues too readily and should be entirely avoided. Now the Syracuse crystal bearing the worms in a small quantity of oil is tipped only slightly and a large drop of pure, unthinned, paper-filtered Canada balsam is placed on the sloping bottom of the dish away from the worms and the whole covered. The resin will flow slowly down and diffuse throughout the oil and specimens in the course of 2 or 3 hours. Should the resulting resinous mixture be too thin to dry rapidly upon mounting the objects, more balsam may be added as before. It is important not to rush this process because the thinner medium within the worms will move through to the exterior faster than the balsam can penetrate to the interior with the result that the pressure becomes less within than without and unless the cuticula is thick, collapsing will result; but in all cases the more volatile fluids will vaporize under this reduced pressure and fill the body cavity and interstices between the organs with gas so that the preparations are again valueless, being utterly opaque. If collapsing has not taken place, the difficulty may be remedied by thinning the balsam with chloroform or benzol until the bubbles are gone, then controlling evaporation until the thickness of the fluid is again suitable for mounting. However, should collapsing have occurred, and should the specimens be valuable enough to warrant saving, restoration may be accomplished by running the worms back to Carnoy-phenol and leaving them there until the collapsed portions have filled out. If this does not occur spontaneously, a slight manipulation by rolling the worm gently will usually restore shape but should this not be the case restoration by the lactic acid method may be used (Hetherington 1922).

Except for low power work with a microscope, toto staining is of little value in examination of relatively large specimens because of the marked

tendency it has to mask the finer details of structure which one is desirous of seeing when using higher magnifications. This is due to the deep and homogeneous coloration taken on by the cuticula and underlying structures belonging to the bodywall. Best results along the line of toto staining using Carnoy-phenol in the process were obtained by using Orange G, safranin, methyl green, lichtgrün, acid fuchsin, methyl blue, Mayer's HCl carmine and Ehrlich's hematoxylin.

With the exception of HCl carmine, safranin, and the hematoxylin, all these stains are used by adding the dry powder in very small amounts to Carnoy-phenol and the degree of staining controlled. Safranin is utilized to saturation in 70 per cent alcohol and allowed to strongly over-stain the specimens. Then they are removed to Carnoy-phenol until destaining is sufficient when clearing is at once undertaken. Acid fuchsin is the most tenacious of the stains mentioned and colors very rapidly. The most presentable mounts were obtained by slightly overstaining the specimens in the phenol reagent with small quantities of acid fuchsin and lichtgrün added in powder form to make a dark purple solution. Then the cuticula and body-wall musculature are destained by placing the worms in 95 per cent alcohol and passing into it a small quantity of dry ammonium gas. When all color is totally gone and the specimens are white showing no clouds of red coming off, they are returned to pure reagent which again restores the red color, most of which is now only in the internal organs. Clearing and mounting are done as described previously.

Much greater latitude for observation is better obtained by utilizing degrees of clearing rather than staining. Permanent mounts may be made of glycerine-prepared specimens in glycerine jelly properly sealed against evaporation, or material may be mounted after suitable preparation either in camsal-balsam, cedar immersion oil, or Canada balsam. These four mounting media will give a differential clearing indicated by the following approximate indices of refraction: 1.476, 1.47, 1.520, and 1.535 respectively (Lee 1913). To prepare the specimens for passage into these media, they are first placed in Carnoy-phenol and then brought into the clearing fluids most suitable for passage into the mounting medium. For glycerine jelly mounts, the phenol reagent is replaced by pure glycerine; camsal-balsam is preceded by clearing the material in camsal, a liquid formed by the mutual solution of salol (phenyl-salicylate) and gum camphor; immersion oil follows thin cedar oil; and Canada balsam replaces oil of wintergreen. The process of clearing is accomplished as previously explained.

Another excellent medium for small, very transparent worms is "Diaphane," a resinous medium employing gum sandarac on the order of Gilson's "Euparal" which, because of its low index of refraction, shows greater detail in the cleared specimens than balsam. The nematodes are

cleared carefully from the phenol reagent by camisal and allowed to harden for a short time in this fluid. Then they may be transferred to diaphane, diluted to about one half strength by absolute iso-butyl alcohol, and allowed to clear by gentle evaporation of the alcohol. A slightly greater degree of clearing may be obtained by preparing the worms in the same manner and transferring to pure Canada balsam with 5 to 10 per cent camisal well diluted with iso-butyl alcohol. This, too, makes an admirable, but very slow drying, tough, elastic medium.

SYMMETRY AND STRUCTURE OF THE HEAD REGION

GENERAL CONSIDERATIONS

Type form of the primitive nematode

Ward (1917) has utilized for the purpose of grouping nematodes the structure of the anterior end, particularly the oral armature, and has contrasted three terms: lips, jaws, and capsule, each referring to a typical oral organization. As an example of true lips may be mentioned a member of the genus *Ascaris* (Fig. 42) as showing, when viewed en face, three lobe-like projections of which a large one, bearing two papillae, is dorsal, while the other two each bearing a single papilla, are ventral. The genus *Camallanus* (Fig. 33) illustrates true jaws. Here the armature is divided into dextral and sinistral halves which act as a vise for maintaining a hold on the host tissue. The capsule or third type may be found among the members of the group of *Strongyles* (Fig. 40). Here the vestibule is cup-shaped with a large roomy interior opening to the exterior by an oval or circular orifice. Within the vestibule and on the walls are various organs for cutting, piercing, gnawing, etc. A closer study of the cephalic region, its structure and symmetry may indicate the value of these suggested groupings or may indicate further groupings or means of relating the nematodes within any one category, or still further may serve to show which structure is the most evolved and of the highest type thus indicating the evolutionary status of the species or genus among the members of its genus or family respectively.

In order to obtain the proper perspective of the value of the cephalic structure either from a taxonomic or an evolutionary point of view, it is first necessary to consider what may be termed the primitive nematode, and then in this light determine whether cephalic organization has kept pace with or lagged behind the specialization of the nematode body as a whole, through which it is fitted to its environment. It is for this reason that the primitive nematode is considered in regard to its form and symmetry before the anterior portions of the free living and parasitic forms are discussed critically with reference to their symmetry and specialization in structure.

The great difficulty in such a definition or delineation arises in the determination of criteria for primitiveness. In general a primitive organism is believed to be one with the most generalized structure or in other words

an organism with the most avenues along which it may specialize. However, when one is confronted by a nematode which has organs or a system of organs that are structurally very generalized and at the same time other systems are very highly specialized, the question may be asked whether the simple structures have devolved or are hold-overs of the primitive type which existed in the ancestral nematode. There is naturally no adequate nor absolute solution to such a query and if any explanations are offered they can at best be based only on a critical examination of details in numerous free and parasitic species, each detail being selected with careful consideration of its stability in the stress of environmental factors.

According to Steiner (1919) the type form of nematode body is a spindle in which the principal axis is much elongated over the two similar dextro-sinistral and dorso-ventral axes. Any alterations in the relative proportions of these axes of the primitive form will necessarily alter profoundly the general outline of the body: with extreme lengthening, for example, of the principal axis and only a slight shortening of the other axes, or none, it is a very easy transition into such a filariform individual as an adult *Dracunculus medinensis* Velsch, measuring more than a meter and a half in length. On the other hand, lengthening of the two secondary axes in greater proportion than the principal axis would produce a form of adult such as *Heterodera schachtii* Schmidt, the common parasitic nematode of the sugar beet, the female of which at maturity becomes a swollen lemon-shaped individual.

In cross section the primitive nematode is always circular with no suggestions whatever of dorso-ventral or lateral flattening. Neither is there any evidence of metamerism, a fact which is borne out in extant forms in none of which there is the slightest suggestion of septa. In this connection it should be noted that there is also no coelom, the existing body cavity remaining as a derivative of the primary body cavity or blastocoele. Pseudo-segmentation is present in the cephalic bristles, according to Cobb, of about thirty per cent of the free living nematodes and in one form *Scaptrella cincta* Cobb, even the mandibles are jointed. However, this condition is limited only to the cephalic appendages and in no case, either in the embryo or adult, has any trace of true segmentation been observed in the body proper.

The mouth of the primitive form is terminal as in present forms, except a few genera in which it has become secondarily dorsal, notably in the genera of the family Ancylostomidae. Embryologically the mouth is subterminal ventrally and during development it migrates to the terminal position. There is, however, still a difference of opinion among investigators on this point; some believe that the blastopore as a slit-like opening closes completely from behind forward and that the mouth forms inde-

pendently in front by an ectodermal invagination; other workers believe that the definitive mouth arises from an incomplete closure of the blastopore giving here the ventral location of the mouth which shifts at an early stage to the terminal position. The anus, however, is ventral and posterior, which too is typical of present-day forms barring, for example, a few highly modified individuals such as the adult female of *Heterodera schachtii* with a dorsal anus; *Trichosomoides crassicauda* Bellingham, members of the genera *Trichuris* Roederer, *Eustrongylides* Jägerskiöld, and *Hystrichis* Dujardin, in which the anus is terminal. In free living forms the anus is always posteriorly ventral and a tail is present through the tip of which three caudal glands pour out their secretions. These glands fabricate a cement-like substance which hardens in the presence of water and serves to hold the individual to the substrate of its habitat. The lack of a tail and the presence of a terminal anus as existing in the groups just mentioned do not seem to fit into the conception of the primitive nematode as will appear later in this discussion but they may be of significance in the conception of the ancestor of the primitive nematode, a discussion of which will follow in the course of this paper.

The openings of the reproductive systems of existing forms allow the products of the gonads to reach the exterior differently in the two sexes: by way of the rectum and anus in the male nematode and by way of the vulva in the female worm, an opening quite separate, generally on the ventral surface in the mid-line. It is believed by Steiner that the primitive nematode, male and female alike, possessed only one ventral orifice which was a common opening for the discharge of the reproductive elements and alimentary waste, as well as serving for the outlet of the excretory system. Such a primitive worm possessed a cloaca, which is present now in no known forms; indeed these three systems—alimentary, excretory, and reproductive—terminate in a great variety of positions in extant forms.

Contrary to the hypothetical condition, the excretory system with few exceptions opens mid-ventrally far anteriorly in the neighborhood of the nerve ring. The vulvar opening may be found posterior and terminal in the parasitic nematodes belonging to the genera *Trichuris*, *Heterodera*, *Eustrongylides* and *Hystrichis*, but more often it is near the middle of the worm in free living and parasitic forms alike. In *Syphacia* and some *Oxyurids* it lies far forward in the anterior half of the body—even close to the nerve ring. In the male organisms the gonads open by their ducts into the rectum in connection with the spicular apparatus. Beside these points in the foregoing paragraphs, the primitive nematode has a simple digestive tract, paired gonads, and paired excretory canals. These with all the other elements of the ancestral form are arranged in such a manner that the body is wholly bilaterally symmetrical.

Alterations in bilaterality of primitive type

Among the legion of nematodes existing now, strict bilaterality in which each half of the individual is a mirror image of the other, does not exist as far as known, at least in the adult forms. Some of the immature forms prior to their last moults more nearly approach bilaterality than do any of the adults for in them the gonads are present only in rudimentary form, lying in the mid ventral line. Changes in bilaterality are very easily brought about by any shifting of the relative proportions of the axes: any lengthening of the principal axis without proportionate concomitant increase of the other two axes would for mechanical reason alone produce a serial ordering of elements which had heretofore lain side by side in the body cavity. Evidence of this fact is to be found in the serially arranged testes of many of the free living nematodes and similarly the caudal glands have become serially ordered in a most striking manner (Fig. 22). The female reproductive system exhibits the largest number of variations in arrangement of its parts. The ovaries and uteri are double but the uterine ducts unite so that there is always one vagina and one vulvar opening. In general one ovary is reflected anteriorly and the other occupies the posterior portion of the body cavity, or in cases where the vulva lies far anteriorly or far posteriorly either the anterior or posterior ovary may suffer partial suppression or become entirely vestigial.

Such changes as these just mentioned alter the actual bilaterality but do not in any way change the fundamental bilaterality of the organism. Whatever the changes in symmetry which replace or become superimposed upon the bilaterality of the nematode as a whole, they are secondary features having arisen during the evolution of the primitive form into the present types of great complexity. Strict asymmetry is most noticeably present in the free living nematode, *Bunonema inaequale* Cobb, and in related species which possess on the dextral side a row of immense tubercles giving the individual a curious unbalanced appearance. Such striking asymmetry is not very often seen and in place of it radial symmetry constructed on plans involving varying numbers of radii is much more general. In order to understand better, perhaps, the advent of this type of symmetry, it is necessary to consider the question of the orientation of the primitive nematode with respect to its surroundings. Steiner has discussed this question in considerable detail and his views in main will be outlined in the following few paragraphs.

Primitive orientation of nematodes

Whoever has dealt with free living or parasitic nematodes is aware of the fact that they always lie upon either the dextral or sinistral aspect of the body, so that their looping and twisting is in reality confined to the plane of their principal axis. The morphological ventral surface becomes a

lateral surface so that the actual creeping surface is in no way comparable for example to the creeping surface of the earthworm. The embryological evidence indicates that the actual adult and embryonic ventral surfaces are the same so that there can not have been any shifting of the anal, excretory, and reproductive openings to a lateral field. This fact proves that the mode of locomotion engaged in by most nematodes has been acquired as a secondary means of progression.

The primitive orientation was probably of such a nature that the principal axis was perpendicular to the substratum—the nematode being held in position by the secretions of the caudal cement glands. In this position the nematode could wave back and forth in a dorso-ventral plane simulating the waving movements of some of the tubificid worms. In support of this orientation are examples of some half sessile free-living nematodes (from fresh and salt water) which live on algae and aquatic vegetation and which may or may not possess eye spots. These sense organs are blackish or red pigment spots or pigment cups, each of the latter bearing over it a single transparent lens, as for example in the following worms:

Thoracostoma antarcticum von Linstow

Thoracostoma lobatum Steiner

Nemella ocellata Cobb

Ionema ocellatum Cobb

Onchulella ocellata Cobb (Figs. 21 and 30).

These ocelli with few exceptions are to be found far forward lying laterally upon the esophagus; only in a few cases do they lie slightly dorsal or ventral with respect to the esophagus. The lenses are so directed that light coming from a vertical source will fall upon them when the worm is oriented vertically. Should the primitive worm have moved normally on a side, as many of them do today, one or other of the eye spots would have been turned toward the substrate and would have thus become temporarily useless. Light to have stimulated both spots through the medium of the lenses with the worm so oriented would necessarily have come from a horizontal source which is improbable. Other nematodes, members of the genus *Echilidium*, possess pigment surrounding the esophagus and above this a circlet of ocelli set to collect vertically falling light.

Furthermore some free living nematodes possess many long delicate cephalic bristles, (*Monhystera pilosa* Cobb (Fig. 13), *Pomponema mirabile* Cobb) and others bear on their bodies many fine bristles (*Sphaerolaimus hirsutus* Bastian, *Notochaetosoma tenax* Irwin-Smith). These delicate processes can not be reconciled with a creeping mode of locomotion through sand, mud, and debris, but they are consistent with a half sessile form of existence. Still other species are parasitized by epizoa and epiphytes which cover all portions of the body. For instance, a delicate filiform alga often

covers the body of *Spira parasitifera* Bastian while vorticella may attach itself to the tail of the same worm. Such ectoparasites could neither remain attached to the nematode nor stand the wear and tear if the host thrashed about among debris and sand. According to Irwin-Smith, some members of the family Chaetosomatidae, which however are not clearly true nematodes, hitch along the rocks and vegetation in the manner of measuring worms by means of special adhesive bristles arranged in two rows on the ventral surface near the tail and by other adhesive bristles on the dorsal portion of the cephalic region. Seurat believes these bristles are a special adaptation. Some other free living nematodes according to Cobb's observations move as many rotifers do, in a looping fashion, using the caudal glands and suction created by the muscular esophagus as alternate means of fixation during progression.

The points reviewed in the foregoing paragraphs seem to indicate rather strikingly that the primitive nematode led a half sessile life, oriented in an upright or nearly upright position, as do many of the free living forms today. Another feature of interest in this connection, the sessile tendency, is the prevalence of radial symmetry in the anterior regions of great numbers of non-parasitic and parasitic forms. A characteristic of sessile animals like the Coelenterata is their radial symmetry, or like the Echinodermata their pseudo-radial symmetry, which has become superimposed secondarily upon their primary bilaterality. As a result of the sessile tendency among the free living nematodes, pseudo-radial symmetry would materially develop.

Definition of the primitive nematode

Steiner (1919) has defined the primitive nematode in short as a bilaterally symmetrical, spindle-shaped animal affixed to its support by the secretions of three adhesive glands at its caudal extremity, possessing a simple digestive tract with no diverticula or convolutions but with a muscular esophagus, having paired gonads in the two sexes lying parallel, one on each side of the intestine, throughout their length, their ducts opening with those of the paired excretory vessels and the intestine into a cloaca discharging by an anus to the exterior in the mid ventral line, slightly anterior to the termination of the tail. Seurat (1920) after a careful consideration of what he believes to be primitive characters still maintained in some of the present day nematodes, avoiding characters induced by adaptation to environment (parasitic adaptations like complex ovejectors, organs of fixation, buccal cavities armed with teeth, or free-living adaptations such as long cephalic bristles, ventral adhesive setae of the Chaetosomatidae, buccal stylets of *Xiphinema* and *Dorylaimus*, etc.), defines the primitive nematode as follows:

"Vermiform organisms of small size living in detritus or decaying

material in moist surroundings; bilaterally symmetrical; mouth subterminal, ventral, limited by three lips, one dorsal and two subventral; tails acutely conical, presenting three caudal glands which open at its point. Cuticula smooth, covered by scattered sensory papillae; epidermis of distinct cells; four bands, dorsal, ventral and laterals, separating four muscular fields; muscle cells of large size, few in number; lateral bands presenting scattered unicellular cutaneous glands.

"Buccal cavity tubuliform, short; anterior intestine (esophagus) elongated with tripartite lumen, lined interiorly by a cuticular membrane, differentiated into a clubshaped esophagus swollen at its terminal portion and a bulb with valves (proventricle); middle intestine of entodermal origin, formed of a small number of large cells, giving forth sometimes a dorsal cecum in its anterior region; terminal intestine short, lined by a cuticular membrane in connection at its origin with three unicellular rectal glands. Excretory apparatus paired, comprising on each side of the body an anterior canal and a posterior canal which come to open by a lateral pore where there also empties a unicellular gland. Sometimes this apparatus is double and admits of a second system of canals opening in the posterior half of the body. (This form is realized in some females of the genus *Rhabditis* opening alone without any single gland by a small pore laterally situated in a band of muscles.)

"Sexes separated; sexual dimorphism faint, the male being characterized simply by a richer development of papillae in the presence of the sexual orifice. Genital glands paired; the two genital tubes of the male being differentiated into testicle, vas deferens and ejaculatory canal opening a short distance in front of the anus and extending in parallel toward the anterior portion of the body; two cement glands empty into the proximal region of the ejaculatory canal; copulatory organs represented by two equal spicules sliding in an unpaired groove (gubernaculum). The female apparatus is formed of two tubes differentiated into ovary, oviduct, uterus and vagina, opening anterior to the middle of the body and extending in parallel course toward the front; ovaries clublike, oocytes not very numerous; uterus serving for storage of a very small number of large sized eggs, borne only to a slight stage of development. The number of genital tubes may advance sometimes to two or even three pairs.

"Eggs homo-lecithal, with clear cytoplasm; segmentation total, unequal. The larva leads a free existence comparable to that of the adult and undergoes four moults in the course of its evolution or growth, its principal increase in size occurring at the moments of these moults, (a character conserved in *Cephalobus ciliatus*). The genital organ is represented in the hatching larva as an unpaired group of two germinative cells and of two somatic cells; this group which remains unpaired throughout

life develops only very slowly in the course of the second half of the larval life."

There are no known living forms which possess all the primitive characters set forth either by Steiner or Seurat. The latter author makes no statements regarding primitive spatial orientation and further regards the three-lipped form—with one dorsal and two ventral lips—as the probable early type while the former author postulates a simple digestive tract devoid of diverticula. Among the free living nematodes members of the genus *Rhabditis* have conserved some of the primitive characters in the structure of the digestive tube and genital organs but have gone far afield in the acquisition of a radial symmetry of the mouth, in the reduction of the male genital system to a simple tube and also in the structure of the lateral lines. On the other hand, among all the parasitic nematodes, those guarding the most numerous primitive features are the members of the oxyurid group. They possess primitive musculature, and show primitive structure of the lateral bands, the excretory apparatus and the digestive tube. Contrary to these ancestral features are the extreme modifications of the ovejector in the female and of the spicular organs and truncated tail of the male. The larvae are, however, rather undifferentiated and afford some of the data upon which the primitive nature of the group is based.

CEPHALIC STRUCTURE IN FREE-LIVING NEMATODES

Symmetrical type of the esophagus

After the preceding discussion of the primitive nematode, its bilateral nature and orientation, the following sections will be limited to a consideration of the structure and symmetrical content of the cephalic region (1) of free-living species, and (2) of parasitic species, in an effort to determine the primitive condition and the successive changes which evolution has imposed upon the early type.

One element of the anterior region which is ever a possessor of triradial symmetry in all the members of the *Myosyringata* Ward (1917) is the esophagus. In cross section, this organ exhibits a triquetrous lumen, "sech-seckig" as Schneider (1866) calls it, with three alternating obtuse angles directed apex lumen-ward, the other three, acute angles, apex outward. Of the three portions into which the muscular tube is divided, one-third is always dorsal and the remaining two-thirds are subventral, so that one of the obtuse angles mentioned is always directed ventrally. The few exceptions existing to this type of esophagus have been placed in the group *Trichosyringata* Ward, a group characterized by the possession of a capillary esophagus. The morphology of such an esophagus has not been carefully worked out so that as yet statements regarding its symmetry and structure are not on a substantial basis. It may be that some of the

genera in that category will have to be removed from it as not being related, such as *Trichosomoides crassicauda* Bell, which, according to Rauther, shows a triquetrous esophagus, at least for a considerable part of the length of that organ.

The triradial nature of the esophagus is such a distinctive feature of the phylum Nematoda and is so nearly universal throughout the group, that it may be accepted as one of the most stable factors in nematode organization. For this reason, it may be considered a primitive feature; certainly, if not primitive, it is one of the earliest features to have been established in the evolving ancestor. When this triquetrous organ, which underlies all the superficial structures of the cephalic region, is used as the basis of determining the symmetry of the head, the only possible symmetrical divisions involving all structures would be two in number; namely, one of bilaterality, and one of triradiality, the latter of which by division of sectors might readily pass into conditions of multiple symmetry among the more superficial structures like the lips. Exceptions to triradiality would, of course, occur in nematodes possessing cephalic branches to the lateral excretory canals, amphids and ocelli. Normally radiality merges progressively into bilaterality as the region of the nerve ring is approached in an antero-posterior direction, suggesting rings or horizontal planes of symmetry appearing at different levels of the cephalic region. The more anterior structures are more truly arranged radially symmetrically while those later succeeding levels as has been said pass into bilateral groupings.

When, however, the more superficial structures of the nematode head and pharyngeal region are examined, these fundamental di- and tri-radial symmetries give place to curious mixtures of symmetrical patterns in one and the same nematode, involving plans based on multiples of two and three radii. Lips, papillae, sensory hairs, cephalic bristles, teeth, and cuticular processes are compounded in a variety of ways; for example, *Oxyuris obvelata* Rudolphi bears three lips arranged in correspondence with the three sectors of the esophagus but the six papillae are grouped in a dextral and sinistral row of three each (Fig. 1). *Protospirura muris* Gmelin carries a right and left row each of three lip-like divisions and four papillae, one at the base of each terminal division of each row (Fig. 10); again, the elaborately constructed *Mononchus gerlachei* de Man, a marine nematode, possesses six radially arranged lips each bearing, centrally placed, a single papilla and at a lower level each carrying two papillae save the two central lateral lips which have again only a single papilla each. Immediately below the lips on the walls of the vestibule are twelve rounded projections of unknown significance. Beneath these there is a chitinous skeletal structure hexagonal in optical section merging into the triangular lumen of the pharynx which itself passes into the ever present triquetrous esophagus (Fig. 3).

These examples were chosen at random from countless other similar, simple and still other beautifully intricate forms merely to show the variations possible, of which the last specimen (*Monochus gerlachei*) illustrates symmetry built on two, three, four, six, and twelve radii. Yet this last whole complex arrangement really becomes bilateral because of the unpaired median lateral papillae and a very large dorsal tooth not previously mentioned, situated on the roof of the buccal cavity about midway between the oral aperture and the esophageal region in the mid-dorsal plane.

Pharyngeal modifications

Turning now to a closer study of cephalic structure, one finds among some of the marine nematodes head regions remarkably simple from the standpoint of structure whereas from the point of view of their genesis they may not perhaps be termed simple in the sense of meaning primitive; however, this point will be reconsidered in another section. In genera belonging to the order Litinia Cobb 1920, there are forms in which the head is devoid of lips; papillae are indistinct or minute; no pharynx is present; the esophagus is simple with no bulb; and cephalic bristles may be absent. *Litotes minuta* Cobb is extremely simple for the mouth opens directly into the esophagus; no lips or bristles are present, but papillae—six in number—exist; the body as a whole is rather simple and the amphids are very indistinct. In *Alaimella cincta* Cobb, the head possesses a simple mouth surrounded by six papillae and probably six flat amalgamated lips which can scarcely be comparable to lips as defined by an example of *Ascaris* in a previous portion of this paper. There are also four cephalic bristles present in this species. A related species, *A. truncata*, the type for the genus *Ailaimella*, has similarly four bristles and six papillae and in the male two testes are present, indicative of a primitive nature. *Ionema ocellatum* Cobb possesses two ocelli with lenses directed anteriorly, a simple circular mouth, no pharynx, no lips, and four cephalic setae. *Schistodera exilis* Cobb and *Tyncnodora pachydermata* Cobb similarly have circular mouths; however, the former bears four minute papillae around the mouth and the latter, two circlets of setae, the first and anteriormost composed of six and the second, of four. Each one of the nematodes just mentioned lives free upon algae and “seagrass” or upon the sand at the bases of this vegetation.

Still other marine forms possessing no pharynx and a simple mouth circular in outline, devoid of any form of lips, are members of the interesting family Chaetosomatidae. These nematodes are not strikingly organized in structure except in the remarkable possession of ventral adhesive bristles on the posterior portion of the body and dorsal cephalic adhesive bristles or setae, which according to observations by Irwin-Smith are utilized in creeping. In this direction these forms have specialized to a

degree. Also the genera *Ionema*, *Schistodera*, and *Nemanema* of Cobb, and *Thoracostoma* Marion have this simple mouth and lack a pharynx.

Next in simplicity are nematodes which not only have a simple circular mouth with none or amalgamated lips, (*Terschellingia longicaudata*, *Monhystera stenosoma*) but also possess a pharynx. The pharynx is one structure which is subject to the greatest diversification and is to a great extent indicative of height of specialization and adaptation in free living forms and also among parasitic species.

Nemanema simplex Cobb, a marine algae-inhabiting nematode, exhibits a very simple cephalic region; bristles are absent; the mouth is a round orifice, surrounded by possibly six exceptionally indefinite papillae, and the pharynx is the merest conoid suggestion. This pharynx, almost unnoticeable in the form above, may become greatly elongated (*Rhynchonema cinctum* Cobb) and constant in width; short and narrow (*Litonema nudum* Cobb); or cavernous and greatly modified as in the genus *Mononchus* Bastian (Fig. 12) notably, and also in many others. The very undifferentiated conoid pharynx and its derivatives attained chiefly by elongation are prominent in nematodes living on a more or less liquid diet. In general, too, the enlarged and widened pharynges are greatly modified by armatures of onchi derived from their walls. Such are to be found among nematodes living upon a solid diet demanding more or less maceration. A very special type of such a pharynx is found among the spear-bearing nematodes obtaining food by piercing and then sucking the fluids, for example, from the roots and tender shoots of either water or land inhabiting plants.

There are, of course, intergradations among the pharynges such that one may arrange a series beginning with nematodes possessing no pharynx (*Litotes*) followed by forms with larger but unarmed pharynx which in turn pass into other forms bearing teeth among which the simpler ones bear three teeth, one each in a position corresponding to the respective sectors of the esophagus (*Mesonchium poriferum* Cobb). The tooth-bearing type, perhaps by further modification, passes into the spear-bearing nematodes such as *Dorylaimus*, *Heterodera*, *Dorylium*, *Eutylenchus*, *Tylenchorhynchus*, etc. Among the *Mononchs* the dorsal tooth is very large and works in opposition to the teeth belonging to the subventral sectors of the pharynx. The teeth on these last two portions may be very small and there may be only one per section as in *Mononchus radiatus*; they may be small and accompanied by numerous denticles (*M. dentatus* Cobb), or by two rasp-like structures approximated near the mid ventral line of the pharynx so that they may operate against the large dorsal tooth (*M. muscorum* Bastian); or further there may be no ventral onchi at all (*M. zschokkei* Mengel). The pharynx is partially mobile in some forms by means of three seams or hinges, one ventral and two lateral and a bit dorsal. In other cases where the walls of the cavity appear immobile, the lips seem

to force the food down upon the teeth and rasps by which means it is torn apart and made ready for swallowing.

Another type of armature is that found in *Synonchium obtusum* Cobb. Here what is apparently the pharynx is highly muscular and forms a large muscular bulb. The mouth is really the large flaring, triangular opening to the pharynx located in a slightly shallow depression formed by the six double, amalgamated, flaring lips. The sectors of the pharynx are equal and each is armed in its mid line by a mandible mounted by three in-pointing teeth and flanked on each side by a small tooth (Fig. 16). When the pharyngeal bulb contracts, the mandibles are approximated, drawn inward and downward while the lips are slightly raised, partly covering the mandibles. Another nematode, *Xyala stricta* Cobb, has three similar but less elaborate mandibles. Still another example of the open flaring and armed pharynx may be found in *Gammanema ferox* Cobb. Here the base of the pharynx is armed with three ribs, each bearing an inward pointing onchium. Jointed mandibles (Fig. 7) are present in *Scaptrella cincta* Cobb, and inpointed ones are again present in *Cheironchus vorax* Cobb and in *Selachinema*.

There are forms which have greatly developed dorsal onchi which have become in many cases much elongated (*Anaxonchia*) and well buried in the esophageal musculature. These spear-shaped onchi are movable and perhaps they form, as Cobb has suggested, the transition from the pharynx armed with onchi to the spear-bearing pharynx. There is still another spear-bearing group in which the so-called stylet is hollow, allowing the fluids to be drawn through it by suction created in the esophagus. *Dorylaimus* and *Discolaimus* are good examples of this construction. Some species indicate by the structure of their stylets that these organs may have arisen by the partial fusion of three onchi and a few of them distinctly show construction from three portions (*Tylopharynx striata* de Man). It may be possible then that by certain developments during the evolution of these trionchiate forms, a partial fusion of the onchi has taken place with an accompanying elongation and narrowing of the pharyngeal cavity giving rise eventually to the hollow pharyngeal stylet. Each of these pharynges has its symmetrical content, but these relations will be considered in a following section in connection with oral structures.

Oral structures among nematodes

The oral structures of the free living nematodes are equally as complicated as the pharyngeal and show almost as numerous variations. The simple circular mouth, noted in connection with some of the nematodes mentioned in a preceding paragraph as possessing no pharynx is, one may say, the simplest from a structural standpoint, but whether it is the most primitive form cannot yet be said. In view of the fact that the esophagus

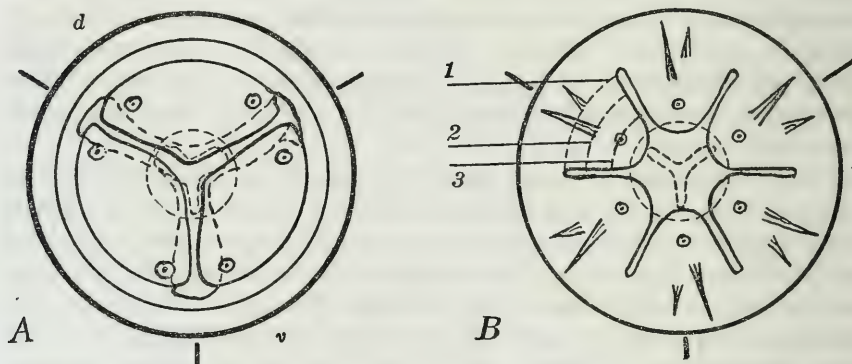
is triquetrous, it would appear that the most primitive form of mouth would not be a circular orifice but rather a triquetrous or triangular opening agreeing in symmetry with the esophagus; however, either view might be taken and some considerations which will follow later will support the former view that the primitive mouth opening was round. In *Thoracostoma setosum* v. Linstow a triangular mouth occurs but in consideration of certain specializations in the head region, it might better be interpreted as a fusion of three lips.

The next structurally simplest form and the one at present conceded most primitive is that found among members of the genera *Enoplus* and *Rhabditis*. The most primitive type of free living nematode in the estimation of nematologists is found in this last genus, where the mouth is surrounded by three lips, which are in fact definite and well formed. One of these is dorsal and the other two are subventral corresponding again with the divisions of the esophagus. The lips may be entire or there may be signs of division as in *Rhabditis pellio* Bütschli where each lip is divided incompletely into two portions by a shallow groove running longitudinally along its mid-region. Similarly *Rhabditis lamaldiensis* Maupas possesses three lips distinctly bilobed, each bearing a pair of prominent setiform papillae, all equal and exhibiting as a whole perfect radial symmetry of the head region.

Quite in contrast to the division of lips may be mentioned the curious labial variations found arising from outgrowths of the lips in the genera *Teratocephalus* and *Cephalobus*. In the species *Teratocephalus crassidens* de Man the six lips surrounding the shallow pharynx have cuticular wings on the edges, partially fused near the bases of these lips, such that there results a corolla-like structure with a continuous edge. The apices of the four sublateral lips bear each a fine bristle (Figs. 2 and 4). On the other hand *Cephalobus ciliatus* von Linstow has arising from each of its three lips a thick column which bifurcates and gives forth two rather long processes whose edges are beset with bristles at regular intervals (Fig. 6). In a position alternating with the lips, the cuticula near the periphery has become elongated into a stout horn-like process. The significance of such diverse outgrowths of lips as represented in the two genera above is not yet known. The radial symmetry of the heads in these two species is only superficial because just below the lip region on the lateral fields lie the amphids, one dextral, and one sinistral. They perforce shift the symmetry to bilaterality.

Evidence gathered from an examination of numerous free living nematodes seems conclusively to show that forms having a small number of lips acquired these labial organs by the subsequent division of the primitive three lips. Six lips are a very common number among many genera and appear as suggested by *Rhabditis* to have arisen by the division of each

of the three lips of the primitive form into two parts (Text figs. A and B). Division, tho incomplete, of these six lips gives rise to twelve lipped forms such as *Anaxonchium litorium* Cobb; complete division, to twelve small lips as *Iotodorus punctulatus* Cobb, and perhaps to the twelve highly modified lips or labial setae in *Pomponema mirabile* Cobb. Division of lips would then indicate a more evolved nature than the three lipped condition. This fact seems to be well borne out because many lipped forms occur among genera which have rather elaborate pharynges (*Mononchus*), and which have specialized in other lines too, like choice of habitat, loss of structures, as caudal glands and of one gonad by suppression. The *Mononchs* are to a large extent land inhabiting predatory nematodes rather more advanced in this last respect than their fresh and salt water relatives. The six lipped condition permits the oral aperture to open widely allowing the mononch greater certainty in seizing its prey and macerating it against the pharyngeal onchi.



TEXT FIG. A. Diagram of nematode head en face showing a simple radial symmetry with three lips. *d*, dorsal; *v*, ventral.

TEXT FIG. B. Diagram showing six lips derived by division of the primitive three. The superficial symmetry is multiradial; the deeper symmetry tri-radial on account of the esophagus. 1, 2 and 3 indicate rings of symmetry previously mentioned in the text: anteriormost, the ring of papillae; next, posteriorly, a ring of long cephalic bristles; and third, a ring of lesser bristles.

While specialization may go in one direction, namely, division of lips, still further specialization even in advance of division results by the union or amalgamation of lips. Degrees of confluence or amalgamation may be easily seen after a survey of a large number of species. For instance, one may begin with a form possessing three distinct lips (*Rhabditis*) and these may then become confluent as in *Monhystrium transitans* Cobb. The mouth opening resulting in such a case is triangular or triquetrous. *Monhystrera stenosoma* de Man seems to indicate this even better than the preceding species. By far the most common number of lips is six, and

they offer many interesting variations, finally becoming confluent and forming a mouth capsule generally in connection with a large cavernous pharynx or buccal cavity. Among the Mononchs as previously mentioned, there are six lips which in many species are very well defined and separated (*Mononchus regius* Cobb) and in others the six lips exhibit various stages of union, for example, in *Mononchus major* Cobb the lips have become more rounded and less distinct so that the mouth opening assumes a hexagonal outline; in another genus and species, *Bolbella tenuidens* Cobb, the mouth has become a perfect circle and the six lips have lost entirely their individuality externally, but internally the organization still indicates the individual lips. An interesting feature, too, of this species is its asymmetry; the amphids, instead of being mid-lateral, have shifted slightly and occupy a dorso-lateral position and contrary to the general rule the dorsal onchus is not the one which has become specialized but instead the sub-medial dextral onchus has elongated and assumed a spear-like nature.

A characteristic feature of the genus *Anguillula* is the entire lack of lips; however, the papillae and internal arrangement of cuticular structures indicate very distinctly that the capsule is the result of completely fused lips, six in number (Fig. 5). In longitudinal section the mouth cavity is definitely divided into two parts; first an upper vestibule, thin walled, with the concave surface facing inward. This portion has probably arisen from the under surface of the fused lips. These organs in many lipped forms have a tendency to become thinner and less distinct so that one might easily expect them to become still less thickened after fusing and losing their identity to a greater or lesser extent. Following this vestibule (in *Anguillula aceti* Müller) there arises the pharynx properly speaking, set off from the preceding structure by a distinct break in the cuticular wall of the buccal cavity (Fig. 14). The lining of the pharynx is much thicker and, as seen in cross sections of the pharyngeal region, the lumen of the canal is triangular. The walls of the canal exhibit cuticular thickenings, one in the mid-line of each sub-ventral sector, which are opposed to a small triangular tooth in the mid-line of the dorsal sector.

A similar distinction between pharynx and vestibule may be seen in *Monhystera stenosoma*. Here the capsule has arisen from the fusion of three lips. Cephalic papillae are not definitely known to exist but the head bears in addition to the two lateral amphids four pairs of submedian bristles, the anterior-most member of each pair appearing slightly shorter than the other.

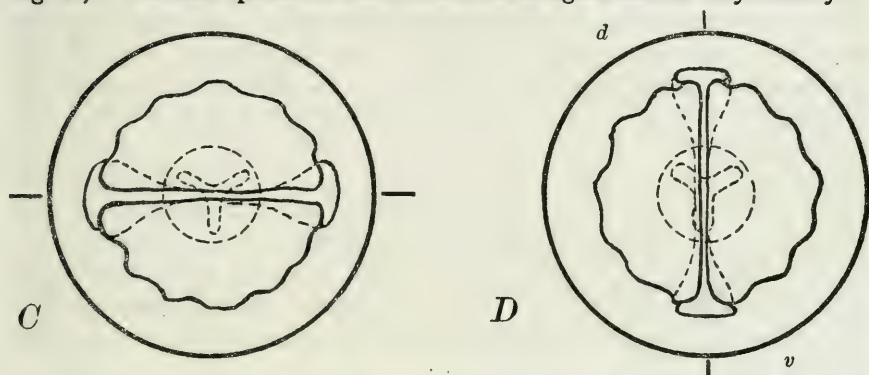
Turning now to a consideration of the oral organization among the spear-bearing nematodes, one finds lips again having undergone fusion either partial or complete. Complete fusion occurs in the genus *Tylencholaimus*, but evidence possibly of labial structure still remains in the presence of six papillae surrounding the mouth. Other genera, *Tylenchus*

and *Dorylaimus*, exhibit the same general structure but some of the species among the numerous ones in the latter genus show distinctly the lip-like nature. The fusion is complete enough to produce a circular mouth opening but the peripheral outline of the crown of lips viewed en face is scalloped showing the external outline of six lips (*Dorylaimus labiatus* de Man). There seems to be in these spear-bearing forms, derived from others possessing armed pharynges, an interesting correlation between extent of lip confluence and pharyngeal specialization. The mononchs with wider but less complex pharynges, from the standpoint of genesis, possess less confluent lips. In this connection one may ask whether the forms cited in an earlier portion of this section as possessing no trace of lips or pharynges have never acquired a pharynx or lips, or whether these structures have been lost by devolution, or whether they may indicate a greater stage of evolution. It cannot be said definitely at present which view is the better one to accept but in consideration of the primitive nature of the gonads in some of those forms it is quite possible that the weight of evidence favors the view of primitiveness.

Another interesting oral and cephalic structure and one which might be interpreted as the forerunner of jaws is to be found in *Synonchium obtusum* Cobb, which was described in connection with pharyngeal modifications. The six double lips have fused completely showing only a continuous crenate rim, as it were, surrounding the large flaring triquetrous mouth and pharynx (Fig. 16). Incidentally this nematode possesses pure tri-radial symmetry as far as the level of the amphids which shift the total symmetry of the head to bilaterality. By the transition from lips to jaws bilaterality becomes the only symmetry in the head region. The apparent change from the bi-radial pharynx to jaws comes through the loss of the dorsal sector of the pharynx accompanied by a lateral shifting of the other two sections. *Selachinema ferox* Cobb illustrates this change very beautifully because there remains a vestigial dorsal sector which, however, is greatly overshadowed by the two powerful submedian chitinous jaws. Another species yet undescribed by Cobb shows no remnant of this dorsal sector. *Chieronchus vorax* Cobb by a similar elimination of the dorsal sector has two jaws or mandibles. *Pseudonchus rotundicephalus* Cobb again supports the formation at least of bilateral mouth parts from the loss of the dorsal pharyngeal sector. So far there is no evidence which supports the view that submedian sectors ever fuse giving rise to jaws which work in apposition dorso-ventrally.

Perfect disymmetry in a dextro-sinistral sense (Text fig. C) is found in the three extraordinary genera, *Diploscapter*, *Wilsonema* and *Heth*, of which *D. coronatus* (Maupas), *W. capitatum*, Cobb, and *H. juli* Cobb are respective examples. The first possesses four strong outwardly directed hooks, two dorsal and two ventral and between them laterally are two

serrated flaps or lips, one right and one left. Cobb interprets in his illustration of this species the two flaps as well as the four hooks, each as a lip. If this is true, the nematode possesses six lips; the two laterals having flattened out and become flaplike; the two dorsals and two ventrals having fused and formed a single dorsal and a ventral double hooked structure. The second species above is distinguished by dorsal and ventral double "combs" and two lateral columns, a dextral and a sinistral one, tipped each by a finer process. Here the disymmetry is most prominent dorso-ventrally (Text fig. D). The last species of the three evinces again lateral disymmetry.



TEXT FIG. C. Diagram of nematode head en face showing disymmetry with respect to a dextro-sinistral plane.

TEXT FIG. D. Diagram showing disymmetry with respect to a dorso-ventral plane. Both this type and the foregoing are forms of bilateral symmetry.

Considerations of symmetry in the head region

After the considerations of esophageal, pharyngeal, and oral structure in the preceding paragraphs, the following ones will be devoted to an examination of the symmetry of the nematode head as a whole, considering the parts played by these structures in determining this symmetry. In view of the fact that the outstanding symmetry of the nematode body as a whole is bilateral, the same relation must have applied to the cephalic region in the primitive form, a fact which seems to be borne out by what is known of nematode embryology, and by features which nematologists have come to accept as primitive. The primitive mouth was ventral and the esophagus arose from three rows of cells, the dorsal one of which was the equivalent of the other two. These features alone would establish bilaterality in the embryo and in the primitive adult.

By an equalization of the three esophageal sectors, the triquetrous and the trisymmetrical nature of this organ became apparent. The primitive nematode had three lips corresponding to the symmetry of the esophageal sectors giving rise ultimately to a purely trisymmetrical structure. Only very few radially symmetrical cephalic regions exist among nematodes

today, because there are in the free living species organs such as amphids and ocelli, and because there are with or without these parts, the cephalic bristles and sensory papillae which in a great number of forms fall into a bilateral arrangement, despite radial ordering of other structural elements. In an otherwise radially symmetrical head, one often finds only four cephalic bristles instead of six, as if the median lateral ones had been lost and in cases of duplication of bristles or papillae on the lips, the lateral median lips are the ones which lag behind the others in this respect.

This peculiarity is well illustrated by Cobb as existing among the mononchs in relation to the labial and cephalic papillae. The arrangement of papillae in these forms follows the law for the arrangement of tactile cephalic setae of nemas in general, namely: ". . . When six are present one is found on each of the two lateral lines and one on each of the four submedian lines; when more than six are present, the increase occurs first on the submedian lines, the commonest number being ten,—one on each lateral line and two on each of the four submedian lines; when the number is in excess of ten, the increase is again more commonly found on the submedian lines." Obviously structures following this order of arrangement shift apparent radial symmetry into bilaterality again. Radial symmetry with few exceptions is actually attainable only if lips alone are concerned, as has already been shown.

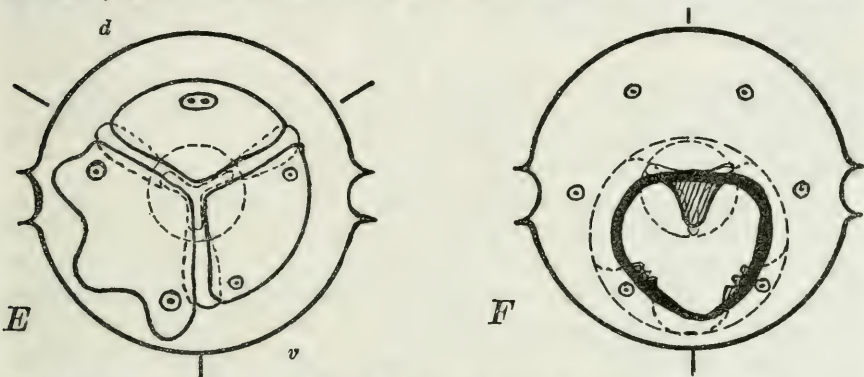
The pharyngeal region is frequently non-radially symmetrical, rarely is this not true, when it becomes armed with onchi (Text fig. F) because the dorsal ones usually have a tendency to surpass in size the other onchi. The small, smooth, prismatic or cylindrical, and unspecialized pharynx readily falls in line with any symmetry which the lips impose upon it. Disymmetry either dorso-ventral or dextro-sinistral exists, as we have seen (Text figs. C and D), in a few free living forms. Its origin is explicable in a few cases as the result of loss of the dorsal lip and pharyngeal sectors. In such cases the cephalic symmetry shifts undeniably into the fundamental bilaterality. Asymmetry occurs least of the other types. In summary it appears then that true radial symmetry is not as general a condition among nematodes as a superficial examination would lead one to expect. Radial symmetry, however, is common, and a striking feature if sensory organs, pharyngeal onchi, and other armatures are neglected or considered secondary in importance to the basic plan of the head region. The apparent order of symmetrical succession in the nematode body beginning with the primitive worm is most probably the following, applied, of course, only to the cephalic region:

1. Primitive bilaterality
2. Radial symmetry (Text figs. A and B)
3. Disymmetry (Text figs. C and D)
4. Asymmetry (Text fig. E)

CEPHALIC STRUCTURE IN PARASITIC NEMATODES

Symmetrical type of the esophagus

What has previously been said regarding the symmetrical factor of the esophagus in free-living nematodes is true of the parasitic forms also, at least those possessing the characteristic triquetrous muscular esophagus. Those nematodes having a capillary esophagus referred to as belonging to the group *Trichosyringata* comprise a restricted number of genera, among them being *Trichinella*, *Trichuris*, *Trichosomoides*, *Capillaria*, etc. Species belonging to these genera have no free-living larval forms and depend for distribution not upon any migratory effort on their own part but rather upon direct transmission of the embryos or eggs into the new host. *Trichina*, as is well known, is spread by the ingestion of the uncooked



TEXT FIG. E. Diagram of a nematode head en face showing asymmetry.

TEXT FIG. F. Diagram showing a typical case of bilaterality in a capsulated cephalic region.

flesh of the host containing the encysted immature worms. The gravid female of *Hepaticola hepatica* Hall dies in the liver tissue of the host, leaving there a mass of eggs which have no way of reaching the exterior or attaining a new host. In such a case, cannibalism seems to be the only agent upon which the species can depend for propagation. From the point of view of such extreme parasitism in this respect and further from the loss of one or both spicules of the male, the absence of one testis and one ovary in the respective sexes and the oviparous or ovoviviparous condition of the female, one might be justified in suspecting that the capillary esophagus is a degenerating one, departing in this respect from the normal form. With regard to the symmetry, this type is bilateral, if the row of large nucleated cells of the structure is dorsal and the capillary tube remains in a ventral median position, or if the tube being intra-cellular, lies within the dorso-ventral plane.

Cephalic modifications and relations to habitat

The transition from a free to a parasitic mode of life brings with it profound modifications in the organism. These changes are most admir-

ably seen when a comparison is made of the fascinating and intricate structure of the head region of free living nematodes with the gross and generally monotonous anatomy of that portion of the parasitic species. Sensory bristles, cephalic setae, ocelli, and other sensory structures as well as the amphids found in free forms are among the first organs to disappear after the assumption of parasitism. Then the digestive system is progressively altered most noticeably in the cephalic region, viz. the oral and pharyngeal structures. Concomitant with the general simplification and loss of structures, there is a rather progressive hypertrophy and complication of the reproductive systems, because as parasitism increases the chances for propagation are less favorable. Further adaptations are seen in the production of cuticular cephalic expansions, as the lateral alae of *Oxyuris tetraptera* von Linstow, the cuticular bosses of *Gongylonema musculi* Neuman, the ventral cuticular combs or spines of *Rictularia*, or the hook beset head of *Echinocephalus*, etc., which are only a few of the possible variations. In a general way, these outgrowths are adaptations which form excellent hold fast organs, as they are found only among those species which inhabit the alimentary canal.

At this point it might be well to consider the possibilities of specialization of the nematode parasite with respect to its habitat. Specialization among the parasitic species is usually the opposite of that among free living forms, for with few exceptions (hold fast organs and reproductive organs) the term implies a simplification or a loss of existing structures. The roundworms living in the posterior and anterior portions of the alimentary system of their host more nearly approach the free living forms than any others. For example, those living in the ceca and large intestine (*Oxyuris*, *Ascaris*) live largely upon the bacterial flora because most of the split proteins and carbohydrates of the digested food have been removed from the intestinal contents by absorption long before these regions are reached. In the stomach little actual hydrolysis of the food is accomplished so that nematodes inhabiting this organ must use and digest to a large extent the food presented them by the host. This fact is demonstrable in *Protospirura muris* inhabiting the stomach of the common mouse, for in this species, the intestine is usually filled by minute fragments and starch granules derived from the host's diet of grains. Other species such as those of *Ancylostoma* actually feed upon the cells of the intestinal papillae according to the observations of Looss.

From a parasitic point of view, the most highly specialized nematodes are those inhabiting the circulatory system (*Filaria*), the body cavity and the connective tissues (*Gongylonema* and *Dracunculus*). They must needs depend for their nourishment upon the absorbed food products circulating in the blood and lymph with which they are bathed and from which they osmotically acquire the necessary elements for their own metabolism. One would expect in such a case to find a correlation between

extent of parasitism in connection with cephalic structure, and such is indeed true as will come out in following discussions.

Pharyngeal modifications

Pharynges among the parasitic round worms are not as diverse in form nor as complicated in structure as many of those in the free living nematodes. There are no intergradations from a simple conoid pharynx, through the various changes of size and armature to the fusion of parts and formation of spears which one finds among the nonparasitic genera. Indeed the pharynges are few and are prominent only among the Strongyles where one finds them exceptionally well developed. The spear-bearing forms exist only among the phytoparasitic nematodes as *Heterodera* and *Tylenchus* but, as these round worms are to a large extent free living, they cannot be adequately classed with the more fully parasitic animal forms.

The simplest pharynx is really little less than a circular vestibule in many species; for example, *Protospirura muris* (Fig. 10) illustrates this quite well as a short cylindrical or faintly prismatic passage leading from the lips into the esophagus. Other instances of such a simple pharynx may be found in such nematodes as *Eustrongylides ignotus* Jägerskiöld and related species. The most elaborate pharynges are, however, found among the Strongyles where they are often large and capacious, almost smooth, or else armed by teeth and cutting plates. These structures are prominent among the characteristic features of the tribes Strongyleae, Bunostomeae, Ransomeae, Cylicostomeae, and a few genera of undetermined tribal relations. But since this capsular formation is so intimately connected with oral structure, its nature will be described in the following paragraphs in connection with modifications of the lip region.

Oral structure and symmetry

When the oral armatures of the parasitic nematodes of the alimentary tract are examined, one finds as a common thing various modifications of lips unarmed or armed with teeth or cuticular thickenings. Three lips are present in the most primitive of parasites, namely genera of the Oxyuridae, Heterakidae and Ascaridae, of which the members of the last family show a great number of modifications. In *Heterakis papillosa* Bloch the three lips are small and equal. A similar equality and tri-radiality exist in *Falcaustra siamensis* Baylis; the lips are somewhat flattened antero-posteriorly except for two prominent papilla bearing projections on each (Fig. 17). *Crossophorus collaris* Hemprich and Ehrenberg, probably an Oxyurid, is tri-symmetrical in every respect save the minor difference between the arrangement of the labial papillae which are two to each lip, but the dorsal lip bears them both at the same level near the lateral borders while the subventral lips carry one papilla a little to the ventral side of the middle of the outer lip surfaces; the other papilla being much smaller

and more anterior with respect to the first (Figs. 15, 37, 28). This might indicate a stage in the disappearance of two papilla, giving way to the more general condition of four cephalic papillae in the ascarids and furthermore this would also make the bilaterality of the ascarid head more pronounced.

Often between the lips of the ascarid type the cuticula and parts of the tissue lying beneath it are raised up into what has been termed interlabia. They fit nicely between the lips and where they are well developed they have been misconstrued as extra lips. The size and form vary from only small projections to a size subequal to the lips themselves as in *Ascaris nasuta* Schneider and *Ophidascaris mombasica* Baylis. Other labial variations arise by branchings of the pulp in each lip into diverse forms (*Polydelphis quadricornis* Wedl) or by partial division into multiple lips from grooves extending longitudinally over the lip (*A. holoptera* Rud. and *A. osculata* Rud.).

An interesting change occurs in the apparent tri-symmetry of the three lipped cephalic structure when diminution of the dorsal sector in some forms and final loss of it in others return the symmetry to bilaterality. The ascarid worms belonging to the genera *Polydelphis* and *Ophidascaris* possess a dorsal lip which is smaller than the ventral ones, and further *Ascaridia columbae* Gmelin shows this peculiarity in particular. It has in addition developed two very large lateral cephalic alae rising at the base of the insertion of the subventral lips and extending as far as the two pedunculated subsymmetrical cervical papillae. The condition of the dorsal lip in such cases seems to indicate that further reduction leads to complete loss of the upper pharyngeal sector or cephalic sector, according to Seurat, as seen in the following genera: *Protospirura*, *Hartertia* and *Acuaria*. *Protospirura labiodentata* Hall (Fig. 31) and *Protospirura ascaroidea* Hall illustrate this condition much better than *Protospirura muris* in which the lips have been deeply cleft appearing, except for the bilateral arrangement, as six separate lips, although their basal regions are partly united by cuticula (Fig. 10).

Undoubtedly a similar condition is present in the family Gnathostomidae whose genera are characterized by two large tri-lobed lateral lips with the cuticula on their inner surfaces thickened and usually raised into tooth-like ridges which meet or interlock with those of the other lips. A curious feature of most of the members of the family is the possession of a head-bulb or cuticular swelling just behind the lips. This bulb contains four submedian, subglobular, membranous structures, the so called "ballonets," each of which is connected by one of the four cervical glands or cervical sacs. The apparent function of these glands seems to be to swell out the ballonets after the nematode has buried its head in the tissue and in this way, with the aid of the interlocking lips, the worm assures itself of a tight hold upon the host organ. The head-bulb may be coarsely striated

or beset with chitinous rose-thorn hooks with their roots buried well in the cuticula; for example *Tanqua tiara* von Linstow (Fig. 25) has five notched lips and coarsely striated cuticula, while *Gnathostoma spingerum* Owen (Fig. 34) has less elaborate lips and a spine beset collar. These forms live with few exceptions within the digestive tract of various animals. Their symmetry is undeniably bilateral as is that of the forms cited in the previous paragraph, and seems to have arisen by loss of the dorsal cephalic sector. In view of the fact that they also show a considerable specialization in the reproductive organs as well as in the cephalic region, one may say that this secondary return to fundamental bilaterality from the apparent radial symmetry of the three lipped forms agrees with the same condition found among the free living nematodes, as has already been demonstrated.

In connection with bilateral disymmetry there are quite a number of forms which would fall into the class of individuals with trisymmetrical cephalic regions if it were not for the development of two very pronounced median lateral anterior alae or the distinctly bilateral arrangement of papillae (*Spiroptera papillosa* Molin, *S. turdi* Molin and *Oxyuris obesa* Diesing, for papillae and *O. tetraptera* von Linstow, for alae). The Camallanidae are conspicuous for their lateral jaws. These consist of two valves similar in shape to Pecten or scallop shells, brownish in color and free only along the dorsal and ventral edges of the anterior halves. Throughout the other half they are fused so that cross sections exhibit a more or less oval chitinous ring. The interior surfaces are ridged and the exterior is covered by a delicate layer of cuticula. Another distinguishing feature of these nematodes is the pair of chitinous tridents, one dorsal and one ventral, articulating with the valves. This type of oral structure is apparently derived from a lip-like structure according to Magath, and Railliet and Henry (1915) have placed the Camallanidae under Spiruroidea, a group which is characterized by lateral lips. As the lateral disymmetry has in other spirurids arisen from loss of the dorsal cephalic sector, the same loss may be responsible for the formation of jaws in Camallanus, as is clearly the case among the free living nematodes already referred to as possessing bilateral jaws or mandibles.

Another oral organization which very closely resembles jaws in appearance and apparent function also is to be found in the genus *Kalicephalus* and perhaps less distinctly in *Diaphanocephalus*, both bursate nematodes of unsettled classification as yet, but according to Stossich apparently belonging to the Sclerostomes. The mouth capsule of *Diaphanocephalus costatus* Diesing is transparent and armed or strengthened by eight cuticular or chitinous ribs running vertically and between these buried deep in the capsule are six papillae. The striking feature of the capsule is that the buccal orifice in place of being circular is a spindle-shaped opening as if the edges of the capsule had been compressed and approximated laterally.

This condition is still more apparent in *Kalicephalus inernus* Molin (Fig. 20) where the capsule is rather more compressed and the appearance of jaws accentuated. The supporting ribs are united anteriorly but are separated posteriad. The exact genesis and significance of this disymmetry and of the jaws in *Camallanus* cannot be known until the larval developments have been carefully examined, but from adult features their similarity cannot be structurally the same.

Turning now to a consideration of parasitic forms which possess cephalic structures arising from a variation of numbers of lips particularly other than three, one finds interesting indications of fusion and capsule formation. The lack of larval and embryological studies on most nematodes makes the problem rather difficult, but as this evidence is unobtainable, conclusions must be based on adult structures. However, as a matter of fact, Seurat has shown in his studies on larval forms that many features of the young do not differ strikingly from those of the adult. The general cephalic structure is often the same, giving little information regarding its evolution. The reproductive systems, however, have been chosen as showing the most phylogenetic facts. Furthermore, in larval comparisons care must be taken to distinguish between structures of apparent phylogenetic importance and those cenogenetic in nature.

Among the oxyurids there are three lipped forms (*O. obvelata*), six lipped ones (*O. hydroi* Galeb), and some with a capsule apparently arising from a fusion of lips (*O. obesa* Diesing and *O. equi* Schrank), and there is even a two-lipped species (*O. monhystera* von Linstow). It is open to question, however, whether the two lipped and capsulated forms are true oxyurids and whether such a diversity of form might not better indicate a generic rather than a specific relationship.

In the family Filaridae the members are characterized partially by their lack of cephalic armature. No pharynx is present; the head is usually rounded with circular mouth opening and with few exceptions no lips are present although cephalic papillae may be apparent existing in the numbers of four and six. Such details would naturally be expected among forms reduced to such a degree of parasitism as these nematodes are. *Filaria bancrofti* Cobbold, for example, has an unarmed circular mouth and two circlets of six low inconspicuous cephalic papillae while *F. candezzi* Seurat is similarly constructed except that the second circlet of papillae contains only four. *Acanthocheilonema diacantha* from the body cavity and lungs of various Brazilian rodents possesses a circlet of six papillae of which the median lateral ones are very large, giving the head a square outline in dorsal or ventral view. A curious feature of the head region of members of the filarid genus *Diplostriaena* (*D. diucae* Boulenger) is the occurrence of two lateral chitinous tridents reminiscent of those in *Camallanus* except that in this latter genus they are dorsal and ventral tridents in connection with the lateral valves.

A slight modification of the filarid head suggesting the possibility of two lateral lips is found in *Setaria equina* Abildgaard, where the mouth is surrounded by a chitinous ring, the lateral portions of which are projected as two semilunar lips. There is as well on the dorsal as the ventral surface a papilliform process and at a lower level on the head there are four submedian prominent papillae. In all the filarid worms just mentioned, with perhaps the exception of the first, the symmetry is bilateral, chiefly so on account of the hypertrophy of the lateral papillae or because of the presence of four submedian in place of six radially placed papillae.

A very noticeable case of radial cephalic symmetry exists in *Spirocera subaequalis* Molin (Figs. 24 and 32) in the adult form. The six denticles of the two lateral lips are regularly disposed around one axis and the buccal border is cut into six equal lobes. This radial symmetry is, however, secondary because in the larval stages of this particular worm, the symmetry is bilateral till the nematode has passed into the fourth larval stage.

In the genera Eustrongylides and Hystrichis, the mouth is usually a triangular or circular opening leading into a very short vestibule similarly shaped in cross section. The buccal aperture is surrounded by six papillae on very prominent projections which have a slight tendency to bilateral arrangement although the radial appearance is more striking. *Hystrichis acanthocephalicus* Molin illustrates this characteristic quite well (Fig. 29). Species of Eustrongylides possess in addition to the six large papillae six to twelve smaller ones, as *E. elegans* von Olfers (Fig. 36).

Finally in the strongylids one finds the most interesting of oral developments in the form of a large armoured buccal cavity or pharynx. The oral aperture is directed often dorsally as in the hookworms or terminally as in the sclerostomes, but of these positions the dorsal location is purely a secondarily acquired one, occurring late in the larval life. *Ancylostoma duodenale* Dubini illustrates very admirably the general plan of such cephalic parts. The ventral margin of the mouth which projects farthest forward carries on each side of the middle line a pair of strong teeth with backward bent prongs. The outer one is always larger and the inner one has near its base on the side turned toward the median plane of the body a small accessory tooth. The dorsal edge of the capsule shows in the middle line a short and rather deep incision of which only the two anterior angles project above the rim, because the greater part of this structure is covered by the cuticula. Upon the ventral wall of the mouth capsule near the base of the cavity is another pair of saw-like teeth projecting freely into the cavity and converging backward only slightly. The dorsal wall of the cavity is pierced obliquely from without inward by the excretory duct of the dorsal esophageal gland.

The whole mouth capsule is one continuous chitinous piece of material which, however, can be changed slightly in shape through the presence in its walls of several sutures where the hard parts are so thin as to permit a

small degree of movement. Internally the capsule is lined by a delicate membrane through which the teeth project from the capsule wall while externally there is a covering of granular material and the cuticula. When variations of this capsular structure arise, it is mainly in the change of form among the teeth and cutting plates. The papillae are six, arranged bilaterally near the edge of the capsule with three on each side (*Ancylostoma caninum* Ercolani Fig. 40).

The head of the larva of the above form is radially symmetrical regarding the triquetrous mouth opening and the papillary arrangement, two to each sector, however the presence of two mid-lateral ridges alters the symmetry to the same as exists in the adult. Indeed, none other than bilaterality could exist in such a structure as the adult capsule. The question of the origin of the capsule can be only partly answered from the larval forms. In the young free-living larva the pharynx is a rather long unarmed tube entered apparently by the triquetrous opening between the three fused lips. If this interpretation is correct, then the buccal capsule arises from a fusion of lips in connection with a large pharynx, as is the case with some of the free-living forms (Figs. 18, 19, 23).

In contrast to the hookworm capsule is the type found among the Sclerostomes which have the mouth opening anteriorly terminal. The general anatomy of the cephalic region is the following: the cuticula or skin is considerably thickened around the edge of the mouth and constricted by a groove which produces a fold of cuticula, the mouth collar. The anterior edge of this structure becomes split up into a very characteristic and delicate fringe which Looss calls the "external leaf crown" the base of which rests on the edge of the buccal capsule. There are six cephalic papillae disposed radially and equally distant from each other. They do, however, shift at times and assume a bilateral arrangement. The medial lateral ones are slightly different from the other four rather submedial papillae which possess cuticular points. The capsule is formed of a homogeneous substance lined by a delicate granular membrane and along the mid-dorsal wall runs the gutter or duct of the dorsal esophageal gland, while at the base on either side there may be two rounded inward pointing plates opposed by two similar ones on the ventral side (*Sclerostomum equinum* Müller) (Fig. 39). These both, however, may be absent or in other genera replaced by three three-flanged teeth arising symmetrically from the floor of the capsule (*Triodontophorus minor* Looss) (Figs. 26 and 38).

The symmetry of the former specimen could not be other than bilateral but of the latter, were it not for the dorsal gutter and a few minor external details, the symmetry would superficially pass as radial. As in previous forms, the striking specific differences arise from modifications of the "leaf-collar," of the general outline of the capsule, and of the armatures arising from the floor and walls of the buccal cavity, but at no time is the symmetry radial in the sense of including other than the most superficial details.

CILATION AMONG NEMATODES

FORMER VIEWS AND PRESENT DATA

It has been a generally held view that nematodes in company with arthropods form the two animal groups totally devoid of cilia at any stage in their existence. Fasten, however, disproved the opinion for arthropods by demonstrating cilia as being present in the reproductive ducts. Shipley in remarking upon the absence of cilia in these two groups believes the condition is correlated with the tendency to form cuticula among nematodes and with the great proclivity for chitinization in arthropods. This view is possibly correct as appears when one examines the variations of intestinal linings among different species of nematodes.

Prenant, who has made a special study of cilia and ciliary modifications, has recently placed in the category of "bordure en brosse" the characteristic intestinal lining of *Ascaris megalocéphala*. An examination of one of his original preparations of the sectioned intestine of this ascarid, showed the lumen-ward end of the cells covered by a thick, rather finely striated border. The elements, however, composing this border are not separately distinguishable for the whole lining is a unit. Just beneath this border is a distinct row of darkly staining basal granules which, too, are more or less confluent and followed by a relatively deep homogeneous zone. This latter portion gives way to the subcentral granular zone through the middle of which is a relatively clear space. The nuclei are basal and lie in a region containing numerous filaments running the long way of the cell. Other authors in treating of this border have pictured the same condition but called it either a cuticular border or a "Stäbchensaum."

Looss found a similar striated border upon the intestinal cells of *Ancylostoma duodenale* but in the cases where individual rods or elements were visible and separate he attributed them to a degeneration of the border, as such were usually seen in adult worms, the younger specimens exhibiting a more united and homogeneous appearance. Such a feature is, no doubt, due partly to the fixation of the material as will be shown later. Martini shows in his studies upon *Oxyuris curvula* identical structures in the intestinal cells (Figs. 46 and 47) and calls the lining a "Stäbchenbesatz." In an alcohol preparation the "Stäbchen" are not clearly separated but in another, a gold chloride one, the lumen ends are apparently free. Following the border is an indistinct layer of basal granules from which fibrils may be traced rather indistinctly into the body of the cell proper. Rauber also in working upon *Enoplus* describes the intestinal

cells as covered by a "Stäbchensaum" (Fig. 43). In his illustration the distinctness of the striae is unmistakable and a splendid basal granule layer is present where each granule is identifiable as well as the fibres running from them into the cell itself.

Another example of apparent ciliation is to be found in *Ichthyonema pellucidum* in the intestinal canal (Fig. 44). Jägerskiöld in describing it states that the lining of this material did not resemble the "Stäbchenlage" of most nematodes because the little rods were widely separated and quite long. He did not, however, examine any fresh material and concludes, "so glaube ich nicht fehlzugreifen, wenn ich es als eine eigenthümlich ausgebildete Stäbchenlage und nicht als ein Wimperkleid betrachte."

An interesting feature of these "bordures en brosse" is that only one author has seen any vibratile motion in the cilia. Cobb (1898) makes this statement: "Toward the end of the seminal vessel, near the ejaculatory duct, the epithelium bears projections having amoeboid movements or cilia having active vibratile motions. This latter interesting fact, first made known by the observer, is of special importance as being the first discovery of a ciliated epithelium among nematodes, a tissue which had been supposed not to exist in the group, and the supposed absence of which had given rise to phylogenetic speculations." He does not, however, present any drawings or name the species in which such a condition occurs and offers no other data in any later papers.

During some observations upon *Protospirura muris*, the author was particularly struck by the apparent beautiful ciliation of the intestinal cells as they appeared in sections prepared from material killed in Carnoy-phenol. Previous examination of sections from specimens killed by Looss' method, showed a more or less hyaline structureless intestinal lining broken into bristle-like portions here and there which, since they were found in mature specimens, were interpreted as degenerating portions of the cuticular lining as Looss had previously interpreted that structure in *Ancylostoma duodenale*. More material was killed in Flemming's mixture without acetic acid and sectioned. The cells exhibited the same discrete ciliation which, too, was present in a very young specimen fixed previous to its last moult. This latter fact indicates that the condition is not due to the age of the specimen.

For further proof of the ciliary nature some fresh, living nematodes were collected and the intestine examined immediately in normal salt solution under dark field illumination and oil immersion. The individual cilia could very plainly be seen in both cases but no motion of their own was ever noted. They would, however, wave back and forth in response to currents of water flowing through the intestine when the slightest pressure shifted the coverglass. The fact that no motion was visible may have been due not to a lack of power of the cilia to beat but to a lack of suitable

temperature conditions or to the absence of calcium salts from the isotonic saline used as an examination fluid—a point not fully appreciated at the time of observation.

In sections (Fig. 45) stained with Dobell's iron hematein one may distinguish the long cilia, an indistinct, rather fused row of basal granules and the fibrils extending into the cell body. Usually the middle portion of the cell is very granular and at times alveolar in appearance so the fibrils disappear but sometimes reappear in the region of the nucleus. Such cells are structurally identical with other ciliated cells and differ physiologically only in the lack of motile cilia.

SIGNIFICANCE OF CILIATION

From a morphological point of view this loss of motion and graded fusion of cilia indicate a retrogression and an atrophy because the divers parts constituting the vibratile apparatus become less and less evident until they are finally obliterated; but from a physiological point of view, this regression, when it is a case of differentiation, is a step in advance, for there results the formation of new organs with new functions. In the case of nematodes the possession of cilia, though they be immotile, is best construed as a hang-over from a more primitive condition of active ciliation. This being the case, the way is open for phylogenetic speculations and a still closer possible relationship can exist then between the nematodes and the rotifers and gastrotricha to which the roundworms at present seem most closely related.

With a ciliated alimentary tract throughout, as rotifers have at present, the ancestral nematode would necessarily have had no need of a muscular sucking esophagus or lips or pharynxes. A simple circular mouth in that case would be the most logical form, such as many of the rotifers possess. Perhaps then the very structureless mouth region of some of the simpler marine nematodes mentioned in the fore part of this paper shows the most primitive form of oral structure, i.e. circular mouth, no lips, indistinct papillae and no pharynx, in contradistinction to the three lipped form described by Seurat as the most primitive condition of oral structure. Loss of ciliation may have arisen by the propensity for cuticularization and by some other unknown change or cause, the simple ciliate esophagus became a muscular sucking organ to carry on the process of acquiring food after ciliary motility had given place to non-motility as evinced by the "bordes en brosse" of species today.

DISCUSSION AND CONCLUSIONS

Regarding orientation of the primitive nematode with respect to its surroundings, Steiner's view that it maintained a position perpendicular to the substrate and followed the half-sessile mode of life seems to be tenable and is well borne out by many of the free-living forms found on and about marine algae and particularly by those worms possessing eye spots with the lenses vertically oriented. The crawling mode of travel engaged in by many nematodes as they lie upon a lateral surface is a secondarily acquired mode of locomotion. Furthermore, the vertical orientation suggests that possibly the ancestor of the nematode, in view of cilia being present, was a free swimming pelagic elongate animal which, after assuming the tendency to cuticularize, settled down to a half-sessile life. The ancestral mouth in the stage with the ciliated digestive tract was possibly ventral and circular, opening into a ciliated esophagus, only slightly muscular or not at all so, and in all probability the anus of such an individual was terminal as well also as the openings of the excretory system. This view is in accord with single openings of these systems spoken of by Seurat in the definition of the primitive nematode. Such an ancestor might easily be derived from a trochophore form by extensive elongation and a partial migration of the mouth anteriorly. Further the symmetry of such an individual would be bilateral which is of course in accord with the fundamental bilaterality of the nematode.

The limiting descriptions of the structural units, lips, jaws, and capsule, proposed by Ward primarily for the parasitic nematodes, are equally applicable to free-living forms, but here there are intergradations from one form to the other so that as a means of grouping the free-living roundworms, these terms are too restrictive and do not permit of placing many intermediate conditions.

From the foregoing discussion and the data in the preceding sections, the following conclusions may be drawn:

1. Cilia are present in nematodes in modified forms and as discrete elements structurally identical with those of vibratile ciliated cells.
2. The nematode ancestor was probably ciliated throughout its digestive tract, and possessed perhaps external cilia, a ventral, simple mouth, and a terminal anus.
3. Loss of external ciliation was succeeded by a half-sessile life and tendency toward cuticularization. The muscular esophagus arose as a pumping organ.

4. The fundamental symmetry is bilateral. True radial symmetry is rare but apparent radial symmetry is very noticeable in the cephalic region and is a secondary condition resulting primarily from the sessile tendency.
5. Disymmetry is tertiary as is asymmetry.
6. The simplest and perhaps most primitive cephalic organization was and is in some forms today, a round or triquetrous mouth opening directly into the triquetrous esophagus, with small or indistinct oral papillae. Successive complication and evolution of structure may be thought of as taking place in the following order:
 - (a) Three lipped forms with no pharynx.
 - (b) Three lipped forms with developing pharynx.
 - (1) Two-lipped forms with no pharynx arising from loss of the dorsal lip.
 - (2) Jaws arising from loss of upper or dorsal cephalic sector and migration laterally of the two subventral sectors.
 - (c) Multiple lips by division of the primitive number.
 - (d) Partial fusion of multiple lips and development of large armed pharynges.
 - (e) Capsule formed by fusion of lips in connection with a large pharynx armed generally by strong onchi.
 - (1) Spear-bearing forms from fusion of lips, elongation of pharynx, and fusion and separation of onchi from the pharyngeal walls to form the buccal stylet moved by special muscles.
7. Disymmetry is more noticeable among parasitic forms than among free-living forms.
8. Cephalic organization has kept pace with other specializations and bears a relation to habitat and is indicative in a general way of the evolutionary status of a genus.

LIST OF FREE-LIVING SPECIES CITED

	PAGE		PAGE
<i>Alaimella cincta</i> Cobb.....	22	<i>Nemella ocellata</i> Cobb.....	17
<i>Alaimella truncata</i> Cobb.....	22	<i>Notochaetosoma tenax</i> Irwin-Smith....	17
<i>Anaxonchium litorium</i> Cobb.....	26	<i>Onchulella ocellata</i> Cobb.....	17
<i>Bunonema ineguale</i> Cobb.....	16	<i>Pomponema mirabile</i> Cobb.....	17, 26
<i>Cephalobus ciliatus</i> von Linstow....	19, 25	<i>Rhabditis lambdiensis</i> Maupas.....	25
<i>Cheironchus vorax</i> Cobb.....	24, 28	<i>Rhabditis pellio</i> Bütschli.....	25
<i>Diploscapter coronatus</i> Cobb.....	28	<i>Scaptrella cincta</i> Cobb.....	14, 24
<i>Dorylaimus labiatus</i> de Man.....	28	<i>Selachinema ferox</i> Cobb.....	28
<i>Gammonema ferox</i> Cobb.....	24	<i>Sphaerolaimus hirsutus</i> Bastian.....	17
<i>Heth juli</i> Cobb.....	28	<i>Spira parasitifera</i> Bastian.....	18
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PLATE I

EXPLANATION OF PLATES

PLATE I

- Fig. 1. *Oxyuris obvelata*. Head of a female en face showing the 3 lips and the 6 papillae disymmetrically arranged. After Flögel. $\times 650$.
- Fig. 2. *Teratocephalus crassidens*. Lateral view showing the peculiar flanged lips. After de Man. $\times 220$.
- Fig. 3. *Mononchus gerlachei*. Head en face showing the 6 partially fused lips, the pharyngeal armature, the large dorsal tooth and the superficial radial symmetry. After de Man. $\times 600$.
- Fig. 4. Same as in Fig. 2, dorsal view. After de Man. $\times 220$.
- Fig. 5. *Anguillula aceti*. Head of female en face, showing fused lips and hexagonal mouth opening. After de Man. $\times 1250$.
- Fig. 6. *Cephalobus ciliatus*. Showing the peculiar prolongations of the lips. After de Man. $\times 220$.
- Fig. 7. Jointed mandibles of *Scaptirella cincta* inflexed and extended. After Cobb. $\times 550$.
- Fig. 8. Optical cross section of the posterior portion of buccal cavity of a growing female, *Anguillula aceti*. After de Man. $\times 1900$.
- Fig. 9. Cross section of pharynx of *Mononchus muscorum* showing the sutures and the dorsal tooth. After Cobb. $\times 400$.
- Fig. 10. Head of *Protospirura muris* showing the disymmetry of the two tri-partite lips. Original $\times 200$.
- Fig. 11. Jointed cephalic seta. After Cobb.
- Fig. 12. Lateral optical section of *Monochus macrostoma*, showing spacious pharynx and large dorsal tooth. After Cobb. $\times 400$.
- Fig. 13. Head of *Monhystera pilosa* showing the delicate cephalic bristles. After Cobb.
- Fig. 14. Head of a growing female of *Anguillula aceti*, showing the break in the pharyngeal wall between upper and lower sections. After de Man. $\times 1250$.

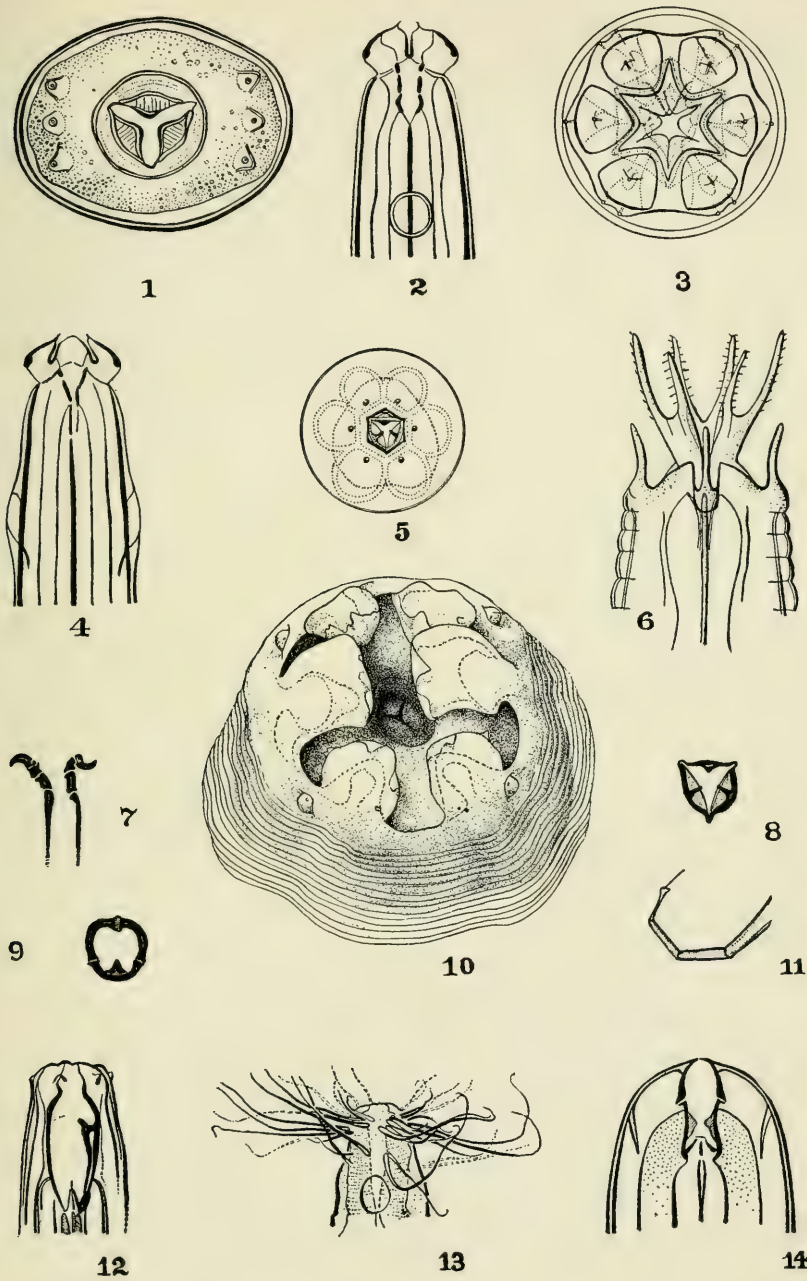


PLATE II

PLATE II

- Fig. 15. *Crossophorus collaris*. Dorsal view showing the fimbriae and the two symmetrically placed papillae of the dorsal lip. After Baylis and Lane. $\times 60$.
- Fig. 16. *Synonchium obtusum*, showing the six double confluent lips, the flaring triquetrous pharynx and its armature of mandibles. After Cobb. $\times 400$.
- Fig. 17. *Falcaustra siamensis*, showing true radial symmetry. After Baylis. $\times 130$.
- Fig. 18. *Ancylostoma duodenale*. Larval head, viewed en face, showing the triquetrous mouth opening, the three fused lips and six papillae. After Looss. $\times 500$.
- Fig. 19. *Ancylostoma duodenale*. Larval head, dorsal view, showing pharynx. After Looss. $\times 330$.
- Fig. 20. *Kalicephalus willeyi*. Front view of head showing the lateral approximation of the capsular edges. After von Linstow.
- Fig. 21. *Thoracostoma chilensis*. Dorsal view of the oesophagus showing the two ocelli with the vertically directed lenses. After Steiner. $\times 370$.
- Fig. 22. *Thoracostoma acuticaudatum*, showing the serial arrangement of the caudal glands. After Jägerskiöld. $\times 80$.
- Fig. 23. *Ancylostoma duodenale*. Larval head, lateral view, showing the tubular pharynx. After Looss. $\times 330$.
- Fig. 24. *Spirocera subaequalis*, showing the radial symmetry of the oral region. After Seurat. $\times 110$.
- Fig. 25. *Tanqua tiara*, showing the collar and the two lateral lips. Dorsal or ventral view. After Baylis and Lane. $\times 110$.
- Fig. 26. *Triodonotophorus minor*, showing the terminal mouth and the three pharyngeal teeth in front view. After Looss. $\times 80$.
- Fig. 27. *Kathleena tricuspis*. Head en face, showing the apparent radial symmetry and the large interlabia. After Gedoelst.
- Fig. 28. *Crossophorus collaris*. Diagrammatic representation of lip and fimbriae relations and symmetry. After Baylis and Lane.
- Fig. 29. *Histrichis acanthocephalicus*, showing the spine beset head and the simple triquetrous mouth with six circumoral papillae. After Jägerskiöld. $\times 80$.

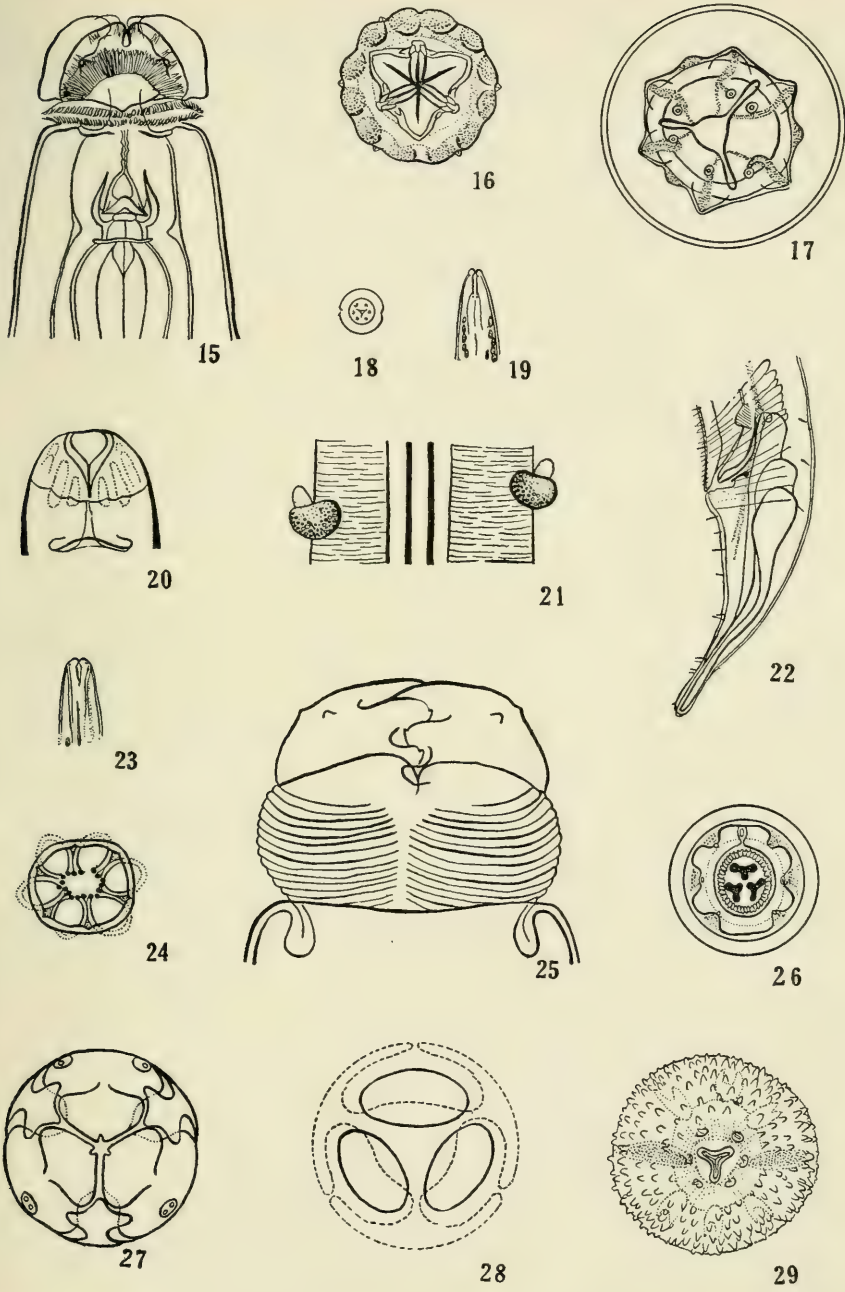
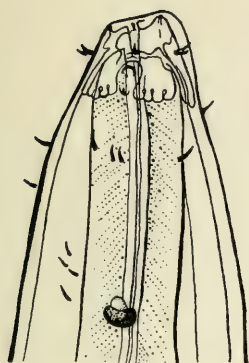


PLATE III

PLATE III

- Fig. 30. *Thoracostoma chilensis*. Lateral view of head showing the location of an ocellus. After Steiner. $\times 370$.
- Fig. 31. *Protospirura labiodentata*. View en face showing the two tripartite lateral lips and the disymmetrically arranged papillae. After von Linstow.
- Fig. 32. *Spirocera subaequalis*, showing the buccal armature. See figure 24. After Seurat. $\times 50$.
- Fig. 33. *Camallanus americanus*. Dorsal view of the oral apparatus of a female showing the two lateral valves and the dorsal trident. After Magath. $\times 80$.
- Fig. 34. *Gnathostoma spinigerum*, dorsal view, showing the two lateral lips and the spine beset head. After Baylis and Lane. $\times 40$.
- Fig. 35. *Kathleena arcuata*. Head en face showing the apparent triradial symmetry and large interlabia. After Geddoelst.
- Fig. 36. *Eustrongilides elegans*, showing the prominent papillae and the slight tendency toward disymmetrical arrangement. After Jägerskiöld. $\times 40$.
- Fig. 37. *Ascaris ferox* (*Crossophorus collaris*). Lateral lip showing the asymmetrical arrangement of papillae. After Schneider. $\times 45$.
- Fig. 38. *Triodontophorus minor*, lateral view, showing the three pharyngeal teeth. After Looss. $\times 80$.
- Fig. 39. *Sclerostomum equinum*, dorsal view, showing the "leaf-crown," dorsal gutter and the large buccal cavity. After Looss. $\times 30$.
- Fig. 40. *Ancylostoma caninum*, showing the ventral teeth and capsule. After Looss. $\times 100$.
- Fig. 41. *Kathleena tricuspis*. Head, dorsal view, showing the interlabia. After Geddoelst.
- Fig. 42. *Ascaris rosmari*. Lips, viewed en face, showing the large dorsal lip. After Baylis. $\times 90$.



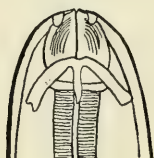
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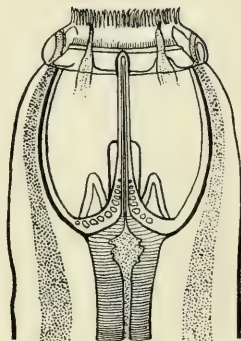
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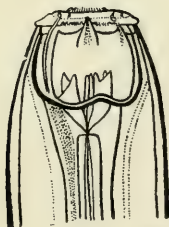
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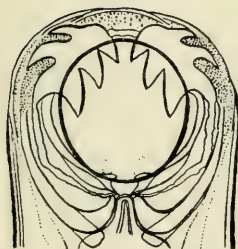
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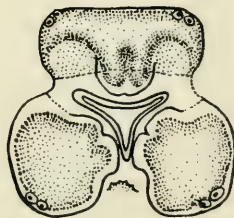
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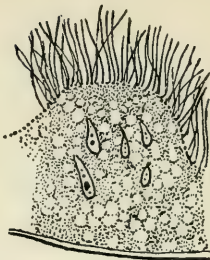
PLATE IV

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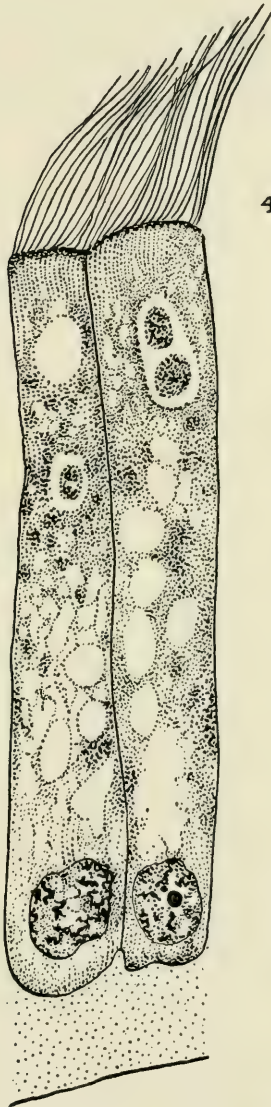
- Fig. 43. *Enoplus* sp. Section of the intestinal wall showing the ciliated border with its basal granules and their fibrillar continuations. After Rauther. $\times 1440$.
- Fig. 44. *Ichthyonema pellucidum*. Section of the intestinal wall showing the separated ciliary structures. Enlarged after Jägerskiöld.
- Fig. 45. *Protospirura muris*. Section of the intestinal wall showing two cells with their long cilia, rather indistinct basal granules and their fibrillar prolongations into the cytoplasm. The dark bodies within the clear spaces are areas infected with *Thelohania reniformis* Kudo and Hetherington, a microsporidian parasite. Original. $\times 2100$.
- Fig. 46. *Oxyuris curvula*. Gold chloride preparation of an intestinal cell showing the ciliary structures. Enlarged after Martini.
- Fig. 47. Same as above. Alcohol preparation showing the "Stäbchensaum." Enlarged after Martini.



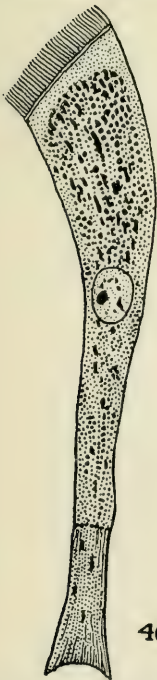
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